Two new amphisbaenians from the Lower Miocene of Kenya

ALAN J. CHARIG

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

CARL GANS

Division of Biological Sciences, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

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SYNOPSIS. Three partial skulls of two new species and genera (*Listromycter leakeyi* and *Lophocranion rusingense*) of Amphisbaenidae, from the Lower Miocene of Rusinga Island, Lake Victoria (Kenya), are described, illustrated, and compared with Recent amphisbaenians. *Listromycter leakeyi* is the largest amphisbaenian known. These new specimens extend the geographical range of the Amphisbaenidae into East–Central Africa, and they are the first fossil amphisbaenians of any age to be found in Africa.

INTRODUCTION

In 1947 the late Dr L. S. B. Leakey collected a quantity of vertebrate material from the Lower Miocene deposits on Rusinga Island, in the Kenyan waters of Lake Victoria. Three years later, in 1950, some of this material was sent to the British Museum (Natural History) in London; it included three small, very unusual skulls. All are broken and incomplete. The first, much the largest of the three, lacks the occiput and the lower jaw. The second and third lack the anterior portions and the lower jaw, each consisting of little more than the actual braincase. Yet there is just enough overlap between the first and the other two to indicate that the first is entirely distinct. The two smaller skulls, on the other hand, seem to be conspecific with each other.

The skulls were first recognized as amphisbaenian by the prominent median tooth in the first skull, the great solidity of the bones in relation to the size of the skulls, the lack of bony arcades, and the marked cranio-facial angle. However, more important as indicating that these animals could not be anything other than amphisbaenians were the extremely heavy premaxilla with its prominent facial process; the relatively few teeth and their relatively enormous size; the frontals completely surrounding the anterior end of the braincase; the peculiar interdigitating sutures between the elements comprising the braincase, resulting in a 'sandwich' construction of the latter; and, finally, the presence of a prominent processus ascendens of the supraoccipital fitting into a median notch behind the parietal. These characteristics and the general concordance between the architecture of the skulls and that of other amphisbaenians left no doubt that all three skulls had been properly assigned to that group.

The description of new genera of fossil amphisbaenians poses certain problems at present. Although the taxonomy of Recent species has now been reviewed (Broadley & Gans 1969, 1975, 1978a, b; Broadley, Gans & Visser 1976; Gans 1967a, b, 1971a, b, 1976, 1987; Gans & Alexander 1962; Gans & Broadley 1974; Gans & Kochva 1965; Gans & Kraklau 1989; Gans & Latifi 1971; Gans & Lehman 1973; Gans & Rhodes 1967), problems in the cranial osteology of the entire group have only recently been addressed (Bellairs & Gans 1983; Bellairs & Kamal 1980; Gans 1978; Jollie 1960). Numerous workers have illustrated amphisbaenian skulls (see Gans 1978 for references), but most of them have studied the same few species. Thus our knowledge of the skull in the species group *Monopeltis–Dalophia*, comprising 23 species, is based entirely upon four descriptions of *Monopeltis capensis* (Peters 1882; Zangerl 1944; Kritzinger 1946; Vanzolini 1951a). More extensive and detailed descriptions are being prepared.

Because of this the present paper can do little more than document the existence of the Kenyan material and describe it as fully as possible. We do include a brief discussion of the presumptive places of the new forms within the amphisbaenian radiation. Yet this analysis rests primarily upon the admittedly incomplete results of the generic review of the Amphisbaenia; it should therefore be regarded as preliminary.

ABBREVIATIONS

The following abbreviations are used in annotations of line drawings, Figs 2, 5 and 6.

bo	basioccipital
c_1	unidentified canal in premaxilla
c_2	unidentified canal in septomaxilla
ec	ectopterygoid
eo	exoccipital
f	frontal
fm	foramen magnum
f_o	foramen, presumably for the optic nerve
f_1	
f_2	unidentified foramina in maxilla
f_3	
f_4	unidentified foramen in posterolateral corner of nasal
f_5	unidentified foramen in anterior tip of vomer
f_6	unidentified foramen between palatine, pterygoid, maxilla and prefrontal
f_7	facial foramina for the VIIth nerve
g_1	unnamed groove extending forwards from the foramen for the Gasserian ganglion
m	maxilla
n	nasal
ocot	occipito-otic complex
op	opisthotic
os	orbitosphenoid
p	parietal
pbs	parabasisphenoid
pl	palatine
pls	pleurosphenoid
pm	premaxilla
pr	prootic
prf	prefrontal
pt	pterygoid
sm	septomaxilla
soc	supraoccipital
stp	stapes
v	vomer

SYSTEMATIC PALAEONTOLOGY

Suborder **AMPHISBAENIA** Gray, 1841
Family **AMPHISBAENIDAE** Gray, 1825

Genus *LISTROMYCTER* nov.

NAME. Greek λίστρον, spade, shovel; μυκτήρ, nose, snout. Refers to the spatulate rostrum, so well developed in the genus.

DIAGNOSIS. Large amphisbaenian with fairly short skull, dorsoventrally compressed snout and strong cranio-facial flexure; sutures well delineated; large median premaxilla with vertical process exposed in skull roof as long, broad bone extending forwards to form powerful spatulate rostrum and backwards to separate nasals entirely and frontals partly; nasal short, with concave anterior edge, extending not so far forwards as maxilla and premaxilla and thus producing embayment in dorsal view; external naris directed anteriorly, just below nasal embayment; premaxilla with one median tooth and three lateral teeth on each side; each maxilla with row of five teeth lying medial to line of premaxillary tooth row, and with stout stubby process directed anterolaterally from front end of its outer side; highly sinuous fronto-parietal suture; prefrontal partly outside and partly inside orbit; large braincase with marked sagittal crest; gap between parabasisphenoid and vomer, exposing orbitosphenoid in palatal view.

TYPE SPECIES. *Listromycter leakeyi* sp. nov.

Listromycter leakeyi sp. nov.

NAME. In honour of the collector, the late Dr L. S. B. Leakey.

DIAGNOSIS. As for the genus *Listromycter*, of which *L. leakeyi* is the only known species.

MATERIAL. Only the **holotype**, Nat. Hist. Mus. Palaeont. Dept. no. R.8292 (collector's field number 375A): skull lacking the occiput and lower jaw. Figs 1–2.

OCCURRENCE. Lower Miocene of Rusinga Island, Lake Victoria, Kenya.

Skull (general description)
The skull appears to have been larger than any other amphisbaenian skull known, fossil or Recent. It lacks the occiput and lower jaw; but the preserved portion, 29·5 mm long, extends backwards as far as a clean transverse break through the braincase (at the level of the middle of the pterygoids) and is reasonably complete. The upper surface and sides of the skull are in excellent condition, free of matrix and with well delineated sutures; most of the sutures and the surface sculpture may be distinguished without difficulty from the fracture lines, which are fairly abundant on some parts of the skull. The lower surface, on the other hand, was formerly obscured by a layer of soft buff-coloured sandstone, through which protruded the upper teeth. Careful treatment with dilute acetic acid has removed this sandstone and revealed a palate in as good a condition as the rest of the specimen. The interior of the braincase was cleaned in a similar manner.

The skull, as in all amphisbaenians, is divided into facial and cranial portions. This division is particularly marked on the dorsal surface, where the axis of the facial portion is bent down at an angle of about 50° to the axis of the cranial portion. The dorsal profile of the face, seen in lateral view, forms an absolutely straight line from the tip of the premaxilla to the fronto-parietal suture. From side to side, however, the upper surface of the face is smoothly convex, the rounding starting just above the lower margin of the skull. The ventral profile of the skull, like the dorsal profile, is bent down anteriorly at a point just behind the last tooth; the angle of the bend is rather less (about 30°).

A striking feature of the skull is the unusually large, thickened and spatulate rostral process; its magnitude is emphasized by the relative shortness, posterior position and concave anterior margin of the roof of the narial passage. The lateral limit of the facial portion of the skull is formed by the maxilla. A process projected anterolaterally just lateral to the narial passage, but now only a stump of this remains.

The orbit is not deeply recessed; the posterolateral wall of the facial region forms its anterior margin, the palato-pterygoid shelf forms its floor, and it is open behind. The posterolateral edges of the facial shelf converge backwards; they unite to form a marked sagittal crest which runs along the top of the cranial portion of the skull as far as the posterior break. The braincase is helmet-shaped in transverse section and has extraordinarily thick walls; it rests upon the posterior part of the palate (see below). The premaxillary rostral process projects well forward of the most anterior tooth.

The palatal surface is bounded by a smoothly rounded edge which forms an elliptical arc lateral and anterior to the tooth rows. The dentigerous surface of each maxilla extends medially past the tooth positions and projects like a shelf beneath the side of a wide, high central vault, roofed by the vomers and the palatines; it may be presumed that in the living animal the shelves on either side were united by a continuous floor of soft tissue, enclosing the internal choanal canals. The palatal shelf continues posteriorly beneath the orbit. Here its medial edge twists dorsally so that the shelf inclines at about 30° to the horizontal with its ventral surface facing obliquely inwards and downwards.

The cranial cavity is slightly wider than high at the site of the break; the flexure between the cranial and facial portions of the skull is also apparent within it. The cavity's diameter is least in the region of the anterior limit of the parietal. Immediately anterior to this there is a slight dorsal outpocketing just beneath the external boss which lies where the posterolateral edges of the facial shelf unite to form the sagittal crest. Farther forward still the cranial cavity increases in diameter again, though its axis now runs parallel to the face.

The skull is extremely solidly constructed. Not only are the individual bones fairly heavy, but they also show complexly interlocking sutures. The location of sutures, especially of those within the braincase, cannot be predicted from their appearance on the external surface of the skull. Elements do not meet in butt joints, but instead overlie each other in a complex manner. A lamina projecting from the edge of one element is often grasped between a pair of laminae from the adjoining one; this produces a very rigid 'sandwich' joint.

Dimensions
Length of facial plane: 23 mm. Length of cranial plane (as preserved): rather more than 10 mm. Estimated length of whole skull, measured in a straight line from tip of premaxillary rostral process to occipital condyle: about 36 mm.

Premaxilla (pm)
The unpaired premaxilla is enormous (length 12·7 mm). It consists essentially of a V-shaped tooth-bearing shelf; from the dorsal surface of this shelf rises a large, heavy vertical plate, expanded above into a transverse plate which is extended forwards to form the rostral process and backwards to form a broad complex exposure on the face.

The exposure on the facial plane consists of a more or less rectangular plate between the nasals, produced forwards into the rounded spatulate rostral process (slightly wider than the body of the bone) and produced backwards as an elliptical process which separates the frontals for half their length and is connected to the rest of the bone by an isthmus.

In lateral view the snout is sharply pointed, the angle between the facial plane and the dentigerous ventral surface being approximately 25°. Near and just dorsal to the most anterior tip of the maxilla, the premaxilla is perforated by a round, longitudinally running canal (c_I) which is open farther on the left than on the right side.

The anterior margin of the tooth-bearing portion forms a smoothly rounded but rather shallow rim (continued on either side for the whole length of the maxilla as far back as the orbit). The ventral surface of the premaxilla bears seven teeth arranged in the form of a V – one median tooth at the front, and two rows, each of three teeth, diverging backwards at an angle of 45° to each other. Only the last two teeth on the right side are preserved complete, the others being represented only by their broken bases. The elliptical median
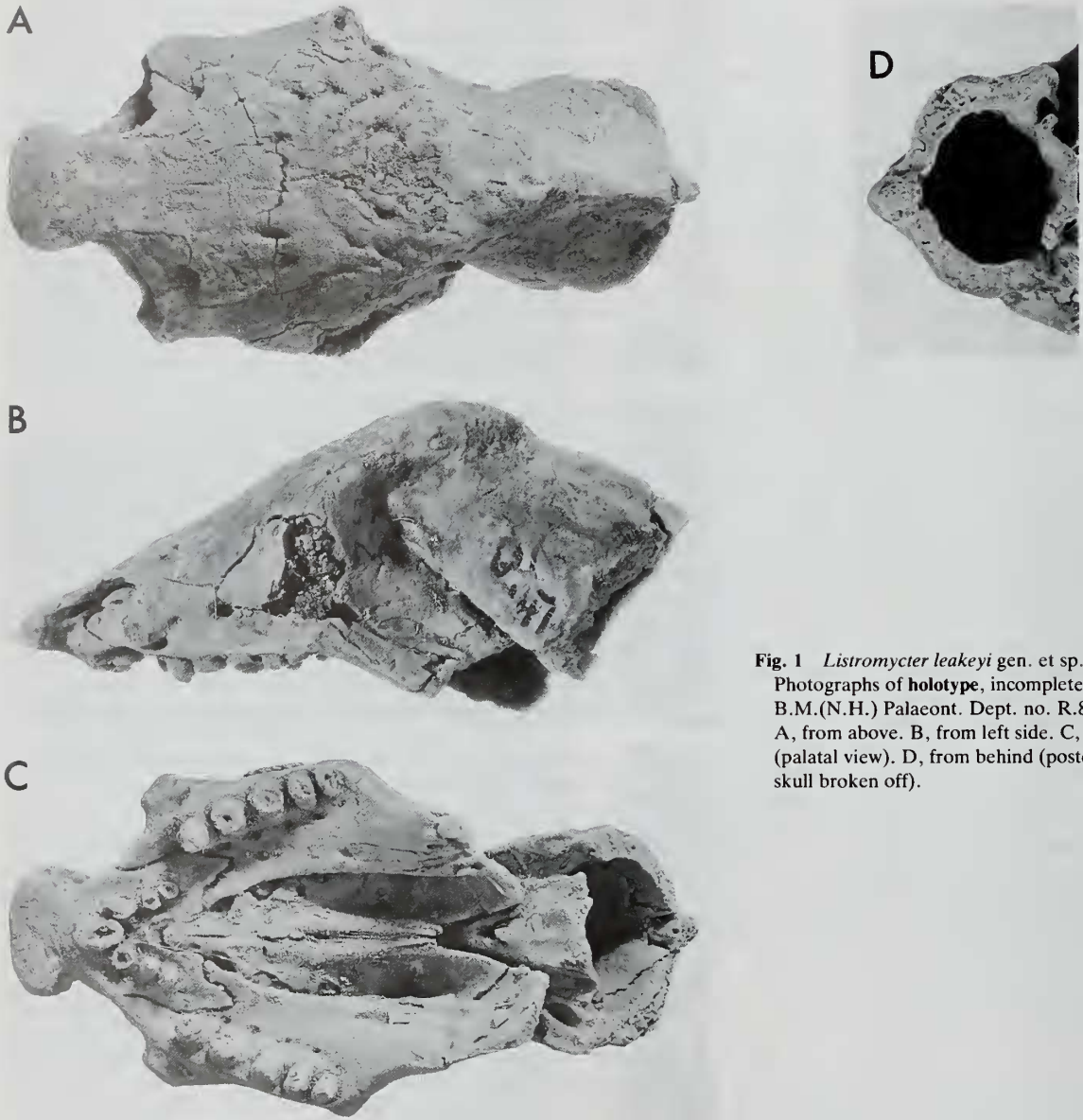
A

D

B

C

Fig. 1 *Listromycter leakeyi* gen. et sp. nov.
Photographs of **holotype**, incomplete skull,
B.M.(N.H.) Palaeont. Dept. no. R.8292, × 3·2.
A, from above. B, from left side. C, from below
(palatal view). D, from behind (posterior part of
skull broken off).

tooth is by far the largest, the long diameter of the base being
about twice that of the first lateral tooth. The second and
third teeth are smaller still. All lateral teeth are circular
rather than elliptical in section. The gap between the first and
second lateral teeth is wider than the other gaps. All these
teeth seem to be straight, bluntish cones with a central cavity.
They are solidly anchylosed to a flat portion of the ventral
surface; the method of attachment appears to be at least as
much acrodont as pleurodont. A nutritive foramen lies
immediately posterior to the medial side of the base of each
tooth.

Maxilla (m)

The maxilla is a very heavy bone. It forms: (a) the palatal
dentigerous shelf, (b) the floor, lateral wall, and part of the roof
of the nasal passage (internal choanal canal), (c) a large part of
the side of the face, up to the frontal suture above and the
anterior rim of the orbit behind, (d) part of the palato-pterygoid
shelf, and (e) a boss projecting anterolaterally. The size and
importance of the maxilla may be gauged by the number (9) and
the extent of its articulations with other elements, namely the
premaxilla, the septomaxilla, the nasal, the frontal, the prefron-
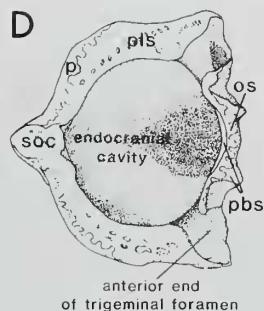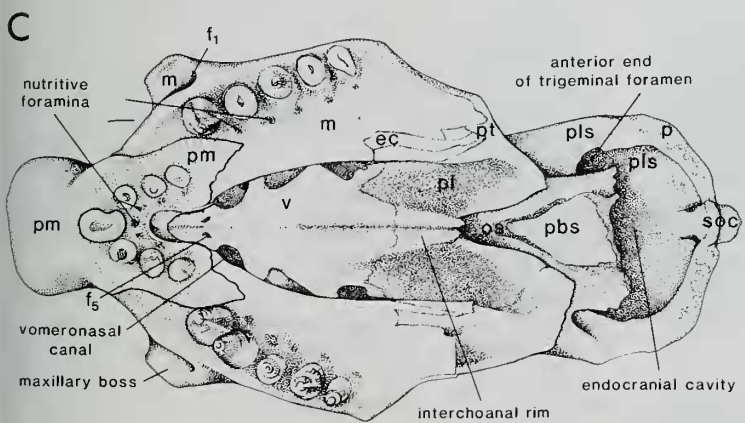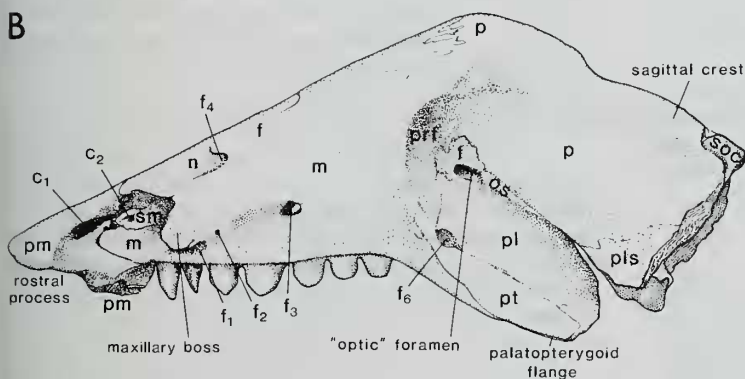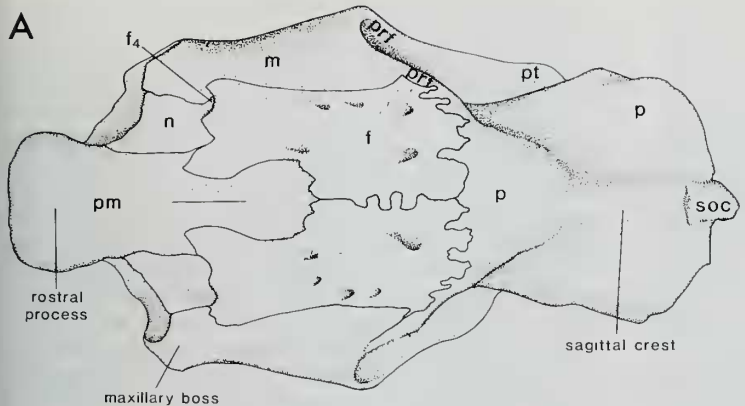tal, the pterygoid, the ectopterygoid, the palatine and the vomer.

Fig. 2 *Listromycter leakeyi* gen. et sp. nov. Drawings, exactly as in Fig. 1. Many irrelevant cracks and breaks have been omitted from these drawings; further, in certain particulars, the left side has been completed from the right (and vice versa). For key see p. 20.

The curved anterior rim of the toothplate, mentioned above with reference to the premaxilla, is continued backwards by the maxilla.

In lateral aspect the maxilla has a roughly triangular appearance, the narrow apex of the triangle being directed forwards. This apex lies immediately beneath the external naris and projects into the premaxilla. Lateral to the naris lies the base of the maxillary boss; ventral to this stump is a horizontally elongate foramen (f_1) and, on the left side only, a smaller foramen (f_2) is present just posterodorsal to the first one. Yet another, even larger, foramen (f_3) may be seen

dorsal to the gap between the second and third maxillary teeth, some way behind the boss. The posterodorsal horn of the triangle which the maxilla shows in this aspect just fails to reach the parietal, the two being separated by a narrow frontal–prefrontal connexion. The posteroventral horn extends down the lateral margin of the palato-pterygoid shelf to underlie the pterygoid in an oblique suture.

In palatal view the maxilla may be seen to bear a row of five teeth just medial to the rim. The line of these teeth does not continue the line of the premaxillary tooth row but, though parallel to that row, lies well outside it. Medial to the teeth

the bone forms a prominent palatal shelf which projects ventral to the internal naris and the vaulted palate; anteriorly the shelf flares inwards to lie dorsal to the maxillary process of the premaxilla and to contact its median dorsal process. Another inward projection of the maxilla lies dorsal to the internal naris and palatal shelf and ventral to the lateral margins of the vomer. The broken posterior edge of the maxillary shelf shows a number of finger-like longitudinal depressions; in one of these lies the slender and elongate ectopterygoid which, anteriorly, almost reaches the last maxillary tooth. The remaining depressions contact what appear to be portions of the pterygoid, though the breaks are very irregular and the element concerned cannot be identified with certainty.

As stated above, five teeth are placed against the marginal rim of each maxilla. The second tooth is the largest, with the first, third, fourth and fifth in descending order of size. The cusps of all except the first left and last right tooth are broken at various levels. The spaces between the teeth are more or less equal. The teeth are elliptical in outline near their bases and are firmly fused to the maxilla in subpleurodont fashion (Gans 1957). The long axes of the ellipses are directed posteromedially. Shallow nutritive foramina lie medial and slightly posterior to the teeth at the point where the extension of the long tooth axis crosses the shallow lingual groove.

Nasal (n)
Each flatly oval nostril is roofed by a small nasal; its anterior edge forms a gentle concave curve. [After the writing of this description an attempt was made to remove more matrix from the cavity of the right external naris. Unfortunately this resulted in damage to the anterior edge of the nasal on that side. We both affirm, however, that this edge was previously a smooth concave curve, complete and apparently natural, as is confirmed by photographs and by the condition on the other side.] The dorsal exposure is roughly quadrilateral, small because the nasal is overlapped by the three adjacent bones. The posterolateral corner of the nasal is depressed into a foramen (f_4) that passes horizontally beneath the anterior process of the frontal and the wall of which also includes a small portion of the maxilla. Erosion of the nasals does not seem to be responsible for the peculiar shovel-shaped appearance of the snout. Certainly the survival of the delicate rostral tips of the septomaxillae argues for a minimum of erosion in this area and suggests that the embayment is natural.

Septomaxilla (sm)
The medioventral wall of the cavity of each external naris is formed by the shell-like septomaxilla, applied to the surfaces of the premaxilla above and the maxilla below. The slender anterior tip projects just beyond the front edge of the nasal; a little behind this tip is the aperture for a canal (c_2) which runs longitudinally back into the bone. The posterior part of the septomaxilla is still encased in the matrix filling the back of the nostril.

Vomer (v)
The vomers lie next to each other along the midline of the palate. Each has a slender anterior projection adjacent to the midline and a blunter posterior projection, and laterally each extends into a flat horizontal plate. The median edges of the vomers appear not simply to end in two straight edges abutting against each other, but to curve sharply dorsad into two parallel plates of unknown extent. In ventral exposure

the vomers occupy an arrow-shaped area between the medial edges of the maxillae. The anterior tips lie ventral to the premaxilla, fitting into a median depression on the underside of that bone and extending as far forwards as the front of the last premaxillary tooth; each tip is perforated by a small foramen (f_5). The lateral edge of each vomer passes directly backwards, turns in towards the midline, and then, at the level of the second maxillary tooth, curves sharply outwards and disappears dorsal to the maxilla; the oval aperture left between the vomer and the maxilla at this point is the opening of the vomeronasal canal (Jacobson's organ). Posterior to this point the roof of the internal choanal canal is formed by the lateral portions of the vomers and, farther back, by the palatines. The lateral edge of the vomer appears once more, however, the bone being embayed to accommodate the supporting process which runs from the medial lamina of the maxilla to the palatal shelf. The straight, slender posterior projection that extends medial to the medial edge of the corresponding palatine forms the interchoanal rim.

Palatine (pl)
The palatine, as seen from below, is a semicylindrical bone forming the roof and sides of the choanal canal. Its lateral edge lies in close contact with, and dorsal to, the medial edge of the palato-pterygoid shelf. From here the bone curves outwards, first swinging laterad, then dorsad and mediad, and finally ventrad to complete the vault. The anterior portion of the medial edge of the palatine lies adjacent to the protruding posterior tip of the vomer and in fact forms the lateral portion of the posterior end of the interchoanal rim. The central portion of the bone is deeply concave. The anterior edge of the palatine lies ventral to the posterior edge of the vomer, projecting forwards so that the suture has a marked angulation of about 90°.

The palatine is broadly exposed in a lateral view of the skull, in which it may be seen to close the orbit ventrally. It extends dorsad from the pterygoid to articulate anteriorly in a complex series of sutures with the prefrontal and frontal, and dorsally with the orbitosphenoid. There is a deep foramen (f_6) close to the point of contact between the anterior tip of the palatine, the pterygoid, the maxilla and the prefrontal (clockwise in that order when viewed from the left).

Ectopterygoid (ec)
A slender rod-shaped ectopterygoid lies smoothly inserted in a furrow on the ventral surface of the posterior end of the maxilla. It extends into and possibly under the pterygoid. The anterior tip of the right ectopterygoid is broken off.

Pterygoid (pt)
The pterygoid forms the posterior portion of the palato-pterygoid shelf. Its anterior tip lies dorsal to the posterior part of the maxilla, with which it is in close and interdigitating contact. The shelf extends medially to the edge of the palatine vault, where both pterygoid and palatine are in contact with the base of the braincase.

Frontal (f)
The frontal is perhaps the most characteristically amphisbaenian element of the skull. Not only is there the usual extensive exposure on the dorsal surface of the skull (i.e. the 'face') and a minor exposure on the lateral wall of the orbit, but, with its fellow, the frontal forms also a complex and reinforced ring around the front part of the brain. It articulates complexly with the parietal and orbitosphenoid behind and

above and with the premaxilla, nasal, maxilla and prefrontal before and below. The following description is based on the external exposures of all these elements and also upon their internal exposures within the braincase.

The smoothly margined anterior wing of the frontal on the facial plane is separated from its fellow by the posterior process of the median premaxilla. The suture between the two frontals and the suture that they make with the parietal across the posterior apex of the 'face' are digitiform and interlock in a complex manner. The exposure of the frontal on the facial surface is markedly rugose; numerous foramina enter the bone, often from the end points of shallow canals.

Within the braincase the articulations of the frontal and the orbitosphenoid are again relatively simple. It may be seen by looking into the braincase from behind that the frontals form the roof, sides and floor of its anterior portion.

The exposure of the frontal on the anteromedial wall of the orbit is also complexly bent, and its margins show evidence of digitiform sutures with the palatine, the prefrontal and the parietal. A large foramen passes between the ventral margin of this exposure of the frontal and the orbitosphenoid; the foramen may be seen to run anteriorly and then curve medially.

Prefrontal (prf)

A short but relatively tall prefrontal forms the anterior wall of the orbit. It articulates laterally with the maxilla; dorsally with the facial exposures of the frontal and parietal; and medially with the parietal, the orbital exposure of the frontal and the palatine. Whether or not there was contact with the anterior tip of the pterygoid is not clear because of the broken condition of the specimen. All the sutures are digitiform.

Orbitosphenoid (os)

The amphisbaenian orbitosphenoid is a median bone that is apparently formed in membrane and may not be homologous with the element thus named in lizards (Bellairs & Gans 1983). It forms all that may be seen of the floor of the braincase in ventral view, except for the forwardly directed triangle in the midline which is the broken-off anterior part of the parabasisphenoid and underlies the orbitosphenoid; on either side lies part of the pleurosphenoid, also broken off behind. Anteriorly the orbitosphenoid is hidden by the palato-pterygoid flanges. It appears also in the lateral view of the skull between the lateral wall of the braincase (formed by the parietal) and the palato-pterygoid flange, extending forwards, between the parietal above and the palatine below, as far as the 'optic' foramen.

Within the braincase it may be seen that its floor is formed by the orbitosphenoid, immediately posterior to the ventral juncture of the two frontals and anterior to the tip of the basisphenoid. The bone is shortest in the ventral midline, where it appears to be faintly grooved as if composed of fused paired elements, though there is no suture line and the grooving appears to be restricted to the internal surface of the bone. The orbitosphenoid is produced anteriorly into a small, square-ended median process, which is clasped on either side by a small, backwardly projecting horn of the frontal. The anterior wings of the orbitosphenoid extend dorsad and anteriorly inwards to the fronto-parietal suture in the lateral wall of the braincase, overlapping that suture medially. Posteriorly the orbitosphenoid extends around the trigeminal foramen on either side, near the anterior edge of which the specimen is broken off. A single small foramen penetrates each side of the orbitosphenoid in the floor of the braincase.

Parabasisphenoid (pbs)

Only the anterior part of the parabasisphenoid is preserved. It appears as a narrow, forwardly directed triangle in the floor of the braincase, seemingly inserted into the back of the orbitosphenoid both internally and externally. In fact, however, the relations are more complex than they seem. The internal exposure obviously consists of a very thin sheet of bone fitting into a shallow, triangular depression on the upper surface of the orbitosphenoid. The external exposure consists mainly of a narrower, thicker, triangular sheet of bone projecting a little farther forwards and fitting into a correspondingly deeper depression, within which it has slipped back a little *post mortem* from its proper position; on either side of this median plate is a very much thinner lateral wing, projecting forwards but not so far. Just how far the orbitosphenoid extended back between these two sheets of parabasisphenoid, rather like the filling in a sandwich, is a matter for conjecture.

The inner suture seems to be radially digitiform on the right side but much straighter on the left; it is difficult to determine which is the natural condition. The cross section provided by the break through the skull indicates that the bone consists of a lamina forming the floor of the braincase, reinforced by a central thickening; the thickening bears three longitudinal external ridges below—a median ridge and, on either side, a lateral ridge which forms the margin of the central triangular plate. The thickened region corresponds to the centre of the interpterygoid vacuity.

Parietal (p)

The unpaired parietal forms much of the roof and sides of the braincase. It is shaped like a squat inverted trough, an inverted U; dorsally it is thickened by the sagittal crest, the anterior termination of which may be detected internally. The nature of the limits of the parietal and of its articulations with the frontals, prefrontals and orbitosphenoid has already been indicated in the appropriate sections above; the complex articulation with the pleurosphenoid and the contact with the supraoccipital are described immediately below.

Pleurosphenoid (laterosphenoid) (pls)

The pleurosphenoid (considered part of the prootic by Rieppel, 1981) appears on either side as a bone that forms a considerable part of the lateral wall of the braincase. Its union with the parietal is highly complex; the external and internal exposure patterns differ greatly, and once again it is obvious that in some places the elements overlap to a considerable extent. The external exposure of the pleurosphenoid on the preserved part of the skull is restricted to the posterolateral corner of the preserved portion of the braincase. Internally, however, the pleurosphenoid exposure extends up the wall of the braincase as far as the dorsal midline, where it makes contact with the supraoccipital. Thus, at the level of the fracture, the lower part of the lateral wall of the braincase consists entirely of pleurosphenoid, but in the upper two-thirds of the wall the thick pleurosphenoid is covered externally by the thin parietal. The cross section shows the pleurosphenoid itself to consist of two layers of dense bone with a central spongy layer and to be separated from the parietal by an undulating suture.

It may also be seen within the braincase that the parietal extends back towards the fracture line and overlaps the pleurosphenoid posteriorly. Thus it is evident that the pleurosphenoid extends farther forwards, hidden between two layers of parietal. On the dorsal side of the brain cavity the

overlapping parietal is produced backwards into a pair of little horns, lying on either side of the supraoccipital and just reaching the level of the fracture posteriorly.

Supraoccipital (soc)

The hindmost tip of the preserved part of the sagittal crest is occupied by a separate bone, the anterior portion of the supraoccipital. Its suture with the parietal, as seen in the section of the skull afforded by the break, does not run straight through the thickness of the bone but forms an S-shape. Just anterior to the supraoccipital there is a wedge-shaped gap which may originally have been filled with cartilage, as in many Recent forms.

Phylogenetic position

Vanzolini (1951*b*) proposed a new subfamily of the family Amphisbaenidae, the Rhineurinae, characterized by a strong cranio-facial angle, a horizontally flattened face and a shovel-like snout. This classification was accepted in such standard works of reference as those of Hoffstetter (1955) and Romer (1956). Gans, however, suggested (1967*a*, 1974) that the various members of the 'Rhineurinae' had developed those same structural features in common because they all shared a style of burrowing called 'shovel-snouted digging' (Gans 1968, 1969) and that, in consequence, the assemblage was almost certainly polyphyletic. Berman (1973) raised the Rhineurinae to family status but separated some of Vanzolini's fossil rhineurines from North America into further distinct families. Gans (1978) accepted the Rhineuridae as a family but, unlike Berman, retained within it all the fossils from North America as well as the single Recent species from that continent; on the other hand, he left all the 'rhineurine' genera from other continents within the Amphisbaenidae.

Gans (1978) recognized also two other families: the Bipedidae (characterized by the retention of hypertrophied forelimbs and other derived characters) and the Trogonophidae (characterized by an acrodont dentition). No 'cladistic analysis' of the Lepidosauria as a whole had at that time been carried out. Gans' classification, however, was based upon a properly conducted character distribution analysis (essentially the same thing) of the genera concerned, and it is now supported further by the results of a wider, as yet unpublished generic/familial analysis.

Listromycter cannot be placed in the Trogonophidae, for its dentition is subpleurodont instead of acrodont. Its skull is very different in other respects; in particular, the cranial suture pattern of *Listromycter* does not accord with the oscillating style of locomotion peculiar to trogonophids. The new genus must therefore be compared with other 'shovel-snouted' extant amphisbaenians, of which there are four genera of Amphisbaenidae (*Monopeltis* and *Dalophia* from Africa; *Leposternon* and *Aulura* from South America) and one single species of the family Rhineuridae (*Rhineura floridana* from North America). *Monopeltis* has 16 species and *Dalophia* 7 (Broadley *et al.* 1976); the present range of neither genus comes closer than 500 km to Rusinga. *Leposternon* has approximately 7 species (Gans 1971*a*) and *Aulura* has but one (Gans 1971*b*).

Aulura is rare and its skull has never been described. The skull of *Dalophia* is also undescribed; in the points mentioned here, however, it is known to resemble that of *Monopeltis*. Indeed, there are only three Recent 'shovel-snouted' species of which the skull has been described: *Monopeltis capensis* from Africa (see p. 20), *Rhineura floridana* from North America (cf. Gans 1967*b*) and *Leposternon microcephalum* from South America (cf. Gans 1971*a*).

The adaptations for shovel-snouted digging in those three species may be arranged under four headings, the first two of which are to some degree related to each other and likewise the last two.

1. *Flattening of the skull*. In all three genera under discussion there is a very marked dorsoventral flattening of the skull, as contrasted with that of the generalized *Blanus* or *Amphisbaena* and even more with the 'spade-snouted' *Anopsibaena* (Gans & Kochva 1965). The dorsal surface, however, remains gently convex from side to side.
2. *Development of rostral shield*. In all three genera the anterior and lateral margins of the upper jaw are extended well beyond the tooth row so as to produce a wide, effective, digging (penetrating) spade with an arc-shaped cutting edge. This extension consists of outgrowths variously formed of the premaxilla and maxillae. A secondary result is the roofing over of the external nares which thus face downwards rather than anterolaterally; this protects them during both the penetrating and the tunnel-widening movements. Yet another effect of the shield development is that the skull appears even flatter than it otherwise would. (Again, contrast this with the conditions in *Blanus* and *Amphisbaena*.)
3. *Flexure of the skull*. The anterior portion of the skull is bent strongly downwards from a point on the cranial roof just behind the fronto-parietal suture. This produces a sharp angulation in the dorsal profile of the skull of between 45° and 70° and a somewhat lesser angulation in the ventral profile, and it results in the ventral deflection of the tooth row from the long axis of the body: in other amphisbaenians the anterior part of the skull is bent down through a much smaller angle (not more than 25°) and the flexure is a gentle curve rather than an abrupt angulation. A marked effect of this is to shorten the ventral perimeter of the skull between the rostral tip and the occipital condyle and, coincidentally, the length of the mandible (see also 4 below).
4. *Shortening of the skull*. In shovel-snouted digging a mechanical advantage is conferred by shortening the distance between the fulcrum and the point of force exertion (thus increasing the forces that may be exerted for whatever moment is generated by the musculature). This may explain the reduction, apparent in all three genera, in the relative length of the entire skull. Since any reduction of the occipital region must be limited by the spatial requirements of the braincase and of the auditory capsule, and since any reduction of the rostral region (the effective digging organ) is also disadvantageous, it is mainly in the anterior part of the cranial region that this shortening takes place.

The combined effect of adaptations 3 and 4 is to shorten the ventral surface of the skull to such an extent that the gap between the parabasisphenoid and the vomer closes entirely. In none of these three genera is the orbitosphenoid exposed in palatal view, and the tip of the cultriform process (the anterior rostrum of the parabasisphenoid) always fits between the posterior processes of the vomers.

Although *Listromycter* possesses all four of these adaptations, it is interesting to note that two of them (nos 2 & 4) are developed to a significantly lesser degree than in any of the three Recent genera:

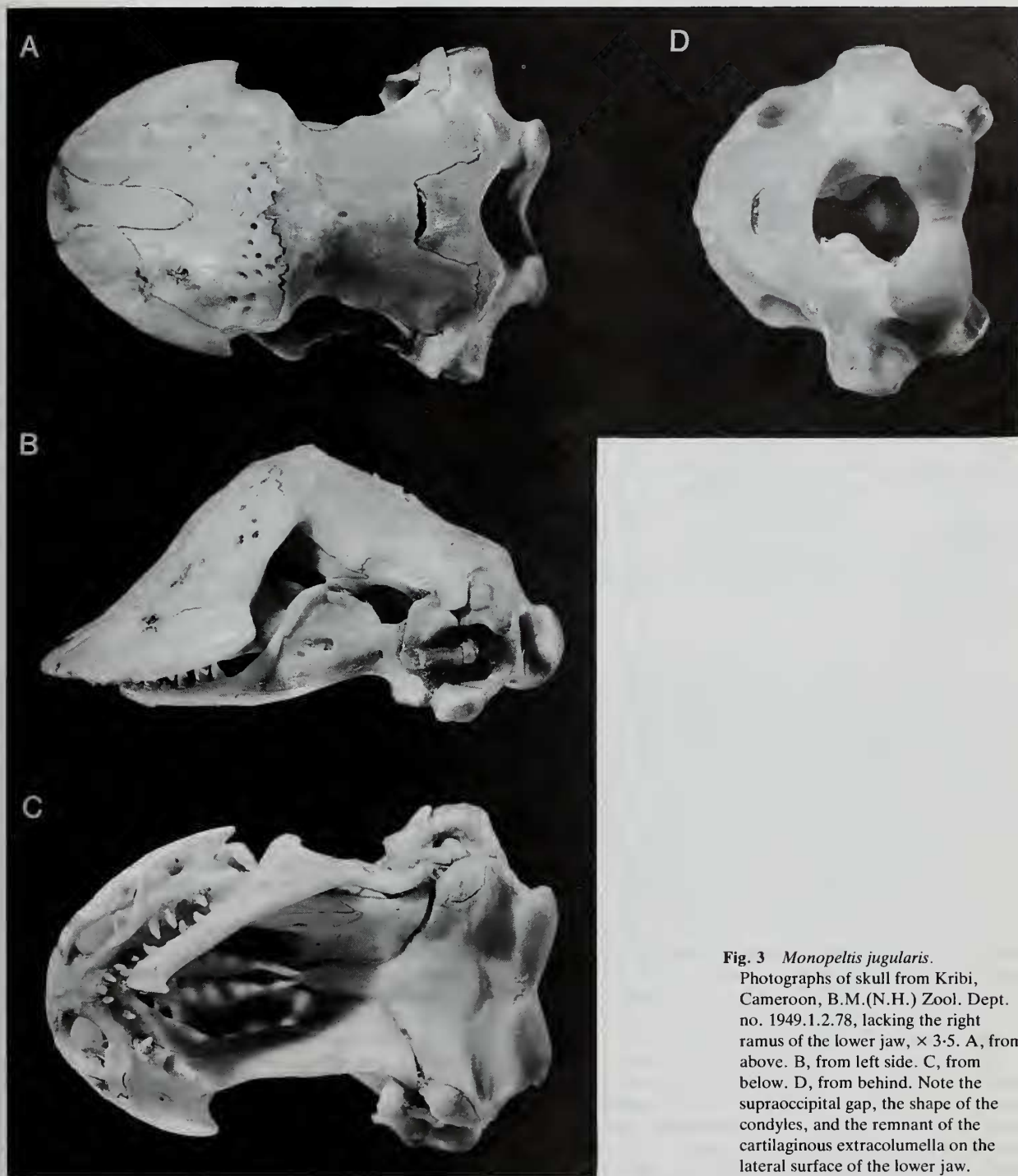1. The skull is flattened to much the same degree.

Fig. 3 *Monopeltis jugularis.*
Photographs of skull from Kribi,
Cameroon, B.M.(N.H.) Zool. Dept.
no. 1949.1.2.78, lacking the right
ramus of the lower jaw, × 3·5. A, from
above. B, from left side. C, from
below. D, from behind. Note the
supraoccipital gap, the shape of the
condyles, and the remnant of the
cartilaginous extracolumella on the
lateral surface of the lower jaw.

2. There is no complete bony rostral shield; but there is a
very large anterior extension of the premaxilla, and each
maxilla bears an anterolateral protuberance of unknown
size (maxillary boss). On the other hand, the maxilla is not
extended laterally beyond the tooth row as it is in *Mono-
peltis*. The external naris, in consequence, is not directed
ventrally; it still faces anteriorly, a little dorsally and a
little laterally, much as in *Blanus*. However, it is possible
that the maxillary bosses in *Listromycter* were connected
by a horny plate, which would have produced an arc-
shaped cutting edge and a downwardly directed external
naris much as in Recent forms.
3. There is a sharp cranio-facial flexure of the skull, measur-
ing 50° in the dorsal profile. This is less than in *Monopeltis*

jugularis (70°), *Rhineura* (65°) and *Leposternon* (60°); but no particular significance can be attached to the size of the angle because it is only 45° in the small *M. capensis*.

4. The skull is shorter than in amphisbaenians which are not shovel-snouted, though not as short as in any of the three Recent shovel-snouted genera listed above.

The figures in Table 1 should not be taken as exact indicators; the parameters chosen have been selected for convenience rather than for their biological significance, and the ratios, which would doubtless vary considerably within a species (especially during ontogeny) are in each case cited for a single specimen rather than given as a mean for a series. Nevertheless they do indicate a trend. In *Listromycter* the gap between parabasisphenoid and vomer is open, *not* closed, and the orbitosphenoid is exposed in the palatal view of the skull.

Table 1   Recent and fossil amphisbaenians. A, ratios of length of facial region to maximum width of facial region. B, ratios of length of whole skull to maximum width of facial region.

Museum and number	Species	A	B
K.M.	*Amphisbaena alba*	1·18	2·79
B.M.(N.H.) R.8292	*Listromycter leakeyi*	1·48	2·40*
C.G. 3722	*Leposternon microcephalum*	1·33	2·30
C.G. 0150	*Rhineura floridana*	1·37	2·10
C.G. 3567	*Monopeltis capensis*	1·16	2·00
B.M.(N.H.) 1949.1.2.78	*Monopeltis jugularis*	1·08	1·69

* length estimated

There is another character in which *Listromycter* appears to be intermediate between 'round-headed' forms on the one hand and the 'shovel-snouted' *Monopeltis* and *Leposternon* on the other. In *M. jugularis* (the largest Recent African amphisbaenid with a spade-snout) [undescribed skull: B.M.(N.H.) Zool. Dept. no. 1949.1.2.78: Fig. 3] the posterolateral corners of the palatal exposure of the premaxilla extend back to beyond the last (4th) maxillary tooth and there contact the ectopterygoid. In *L. microcephalum* the same corners reach back only as far as the middle of the 2nd maxillary tooth and again contact the ectopterygoid. In *Listromycter* and *Rhineura* they extend back as far as the middle of the 2nd maxillary tooth but do *not* contact the ectopterygoid. In forms not shovel-snouted, the posterolateral corners of the palatal exposure of the premaxilla are not extended in this fashion; in *Blanus*, for example, they terminate at the level of the 1st maxillary tooth. We do not understand the significance of this character.

The 'shovel-snouted' *Listromycter*, *Rhineura*, *Monopeltis* and *Leposternon* show remarkably similar modifications of the skull, perhaps as adaptations to a presumably similar mode of life. (As might be expected, those adaptations are less well expressed in the Miocene form than in the three Recent genera.) However, several important differences between the four genera suggest that there is no close phylogenetic relationship uniting them all into one monophyletic group. Can we deduce anything about the more distant phylogenetic relationships that must exist between these shovel-snouted reptiles?

The most striking anatomical differences between their skulls relate to the formation of the rostral process, more specifically the arrangement of the premaxilla, maxilla, nasal,

frontal and external naris. *Rhineura* is unique in that its nasals are in median contact, each of them extending from the anterodorsal border of the external naris to the midline; they are not separated from each other by the backward extension of the premaxilla, as they are in most other Recent amphisbaenians (Gans & Alexander 1962). It is important to note that all the fossil amphisbaenian skulls hitherto described (all of which date from the Lower Eocene or Middle Oligocene of the U.S.A. and have hitherto been referred to the Rhineuridae; references in Gans 1978, Estes 1983) agree with *Rhineura* in this respect. [Other alleged fossil amphisbaenians are *Crythiosaurus mongoliensis* Gilmore, 1943 from the Oligocene of Inner Mongolia and *Changlosaurus wutuensis* Young, 1961 from China. But it seems to us that the former is a primitive boid snake and that the latter is a true lizard.] In *Listromycter*, however, as in *Monopeltis* and *Leposternon*, the nasals are separated by the premaxilla, which, in all three genera, extends so far back as also to effect a partial separation of the paired frontals. In all three genera too the maxilla meets the premaxilla below the external naris. But *Leposternon* differs from *Listromycter* and *Monopeltis* in that its maxilla extends also to meet the premaxilla *above* the naris and thus excludes the nasal from the border of that aperture.

Other characters do not help very much in our present state of knowledge, seeming to be distributed in a somewhat random manner. For example, the fact that a canal enters the posterolateral corner of the nasal in all these forms except *Rhineura* might appear to have some significance, until it is observed that it is present also in *Amphisbaena alba* but absent in *Blanus cinereus*. On the other hand, the frontals are distinctly pitted in all the shovel-snouted forms except *Leposternon*, and again this character is present in *Amphisbaena alba* but absent in *Blanus*. The frontoparietal suture is straight in both *Rhineura* and *Leposternon*, almost straight in *Monopeltis capensis*, wavy in *M. jugularis*, and moderately digitate in *Listromycter*—as it is in both *A. alba* and *Blanus*. One character that is clearly of no taxonomic importance at this level is the tooth count (Vanzolini 1951*a*, *b*); in *Monopeltis capensis* there is but one premaxillary tooth and two in each maxilla (a total of five), and in *M. jugularis* there are seven premaxillary teeth and four in each maxilla (a total of fifteen). *Listromycter leakeyi* retains the maximum (and presumably primitive) tooth count of seven and five—seventeen altogether.

The phylogenetic placement of the Kenyan fossil obviously depends upon the generic arrangement of the shovel-snouted amphisbaenians, a revision of which is now under way. Meanwhile the only reasonable inference that may be drawn is that *Listromycter* is neither a rhineurid, trogonophid nor bipedid but is a member of the Amphisbaenidae; within that family it appears to be on or near the line of ancestry of *Monopeltis* (*Dalophia*) but not of *Leposternon* (*Aulura*). However, it may also be that *Listromycter* represents a separate evolutionary line; we need to examine more species of the *Monopeltis* radiation.

An interesting additional point is that one of the oldest fossil amphisbaenians known, *Jepsibaena minor* (Gilmore & Jepsen, 1945) from the Lower Eocene of Wyoming, has two anterolateral protuberances of the maxilla which are in much the same position as the maxillary bosses of *Listromycter*. In other respects, however, *Jepsibaena* appears to belong to the Rhineuridae, which suggests that the presence of similar structures in *Jepsibaena* and *Listromycter* is due to adaptive convergence.

Genus *LOPHOCRANION* nov.

NAME. Greek λόφος, the crest of a helmet; κρᾱνίον, skull. Refers to the sagittal crest on the skull roof, so well developed in the genus.

DIAGNOSIS. A medium-sized amphisbaenian with weak cranio-facial flexure; slender elongate braincase with pronounced sagittal crest widened just anterior to tip of supra-occipital; transverse crest on supraoccipital; marked lateral expansion of temporal lobe beyond braincase.

TYPE SPECIES. *Lophocranion rusingense* sp. nov.

Lophocranion rusingense sp. nov.

NAME. From Rusinga Island, the only place where the species has been found.

DIAGNOSIS. As for the genus *Lophocranion*, of which *L. rusingense* is the only known species.

MATERIAL. Two incomplete skulls in the Brit. Mus. (Nat. Hist.) Palaeont. Dept. **Holotype**, no. R.8293 (collector's field number not known). Paratype, no. R.8294 (collector's field number 33A). Figs 4–6.

OCCURRENCE. Lower Miocene of Rusinga Island, Lake Victoria, Kenya.

General

Both these fossil skulls were evidently much smaller (see Table 2 for dimensions) than that of *Listromycter*. All that remains of each is the posterior part of an amphisbaenian skull (with occiput and ear region) broken through transversely in front. Amphisbaenian skulls, of course, do not possess bony arcades; both these specimens also lack palato-pterygoid flanges, quadrates and lower jaw, so that each consists of little more than a portion of the braincase itself. As far as can be determined, the two specimens are identical except in that the holotype R.8293 represents a smaller individual than the paratype R.8294 and has better delineated sutures; it is therefore likely to be ontogenetically younger. The skull of the larger individual (paratype) is broken off anteriorly not far forward of the anterior tip of the parabasi-sphenoid; rather more is preserved of the smaller skull (holotype), in which the transverse break runs across the top of the face, just anterior to the highly digitate fronto-parietal suture. Both specimens have been rounded off at the fractures by subsequent rolling.

Despite their incompleteness, however, sufficient of these skulls is preserved—namely, the anterior part of the braincase—to permit a comparison with the corresponding region of *Listromycter*. It is immediately evident that they are quite unlike that genus. In particular, the braincase itself is far more slender and elongate, especially the part between the hindmost processes of the frontals and the anterior tip of the supraoccipital.

The following description is based on the holotype. Any relevant differences observed on the paratype are noted (between parentheses) at the appropriate place; it may otherwise be assumed that the two fossils are alike or that the relevant part of the paratype is missing.

Skull (*general description*)

The cranial region of the skull, just behind the cranio-facial flexure, is transversely narrow. Enough is preserved of the

Table 2 *Lophocranion rusingense*: dimensions (in mm).

	R.8293	R.8294
Length of entire specimen as preserved	11·2	9·1
Length of cranial plane	9·6	–
Transverse width at anterior end of cranial region, i.e. at fronto-parietal suture	3·0	–
Transverse width in middle of cranial region, at widest part of sagittal crest	3·6	5·5
Transverse width across otic capsules	8·4	9·2
Median height of occiput	4·4	5·5
Length of parabasisphenoid	5·3	6·5

apex of the face to indicate that the cranio-facial angle was approximately 20°. The lateral margins of the braincase pass backwards, at first parasagittally and almost straight and then curving outwards at an angle of about 20° to the midline. Just before they reach the back of the skull they sweep out almost laterally to the strongly projecting otic capsules. The much abraded posterior margin of the skull is very roughly convex, the otic capsules lying farther forwards than the occipital condyle. (In the paratype the posterior margin is only slightly convex, but the remaining lateral portions of the occipital condyle project posteriorly beyond this.)

In lateral view the skull as preserved tapers forwards. (The paratype is too short to show this.) The ventral margin is more or less straight, except for its anterior tip which inclines ventrad at some 10°. The dorsal margin slopes gradually downwards as it passes forwards in a smooth convex curve. In this aspect the posterior margin appears as a distorted L (on the right side). The vertical, shorter arm of the L is represented by a backwardly-facing surface; the near-horizontal, longer arm is represented by a surface that faces obliquely backwards and downwards. The obtuse angle of the L would have been formed by the occipital condyle, which is here broken off (but present in the paratype).

There are only two pairs of large apertures and one single one (together with some smaller foramina) in the preserved part of the skull, other than the opening of the braincase at the broken front end. Just beneath the otic capsule, on either side, lies the fenestra ovalis; the latter is closed by the stapedial footplate in these specimens, for the stapes remain in place. Farther forward and directed ventrolaterally is the large, anteroposteriorly elongate foramen for the Gasserian ganglion. The fifth, unpaired aperture is the foramen magnum (fm), in the midline of the dorsal part of the occipital surface and extending right up to its dorsal margin; as far as can be seen, this is a more or less straight-sided quadrilateral, wider above than below. (The remaining fragments of the condyles of the paratype suggest that these originally blocked the ventral third of the aperture as preserved.) On either side of the foramen magnum, at the same height as the lower margin of the aperture as preserved and lateral to the occipital condyle, is a round, much smaller canal, the jugular foramen—actually a compound foramen (see under 'Exoccipital', p. 34). Other smaller, less noticeable foramina will be described below.

The only other prominent feature of the skull is the sagittal crest. This is fairly thick from side to side in the middle part of the cranial region and becomes narrower anteriorly and posteriorly. Although pronounced, the crest is not very high. Midway along its length it bears a triradiate boss which
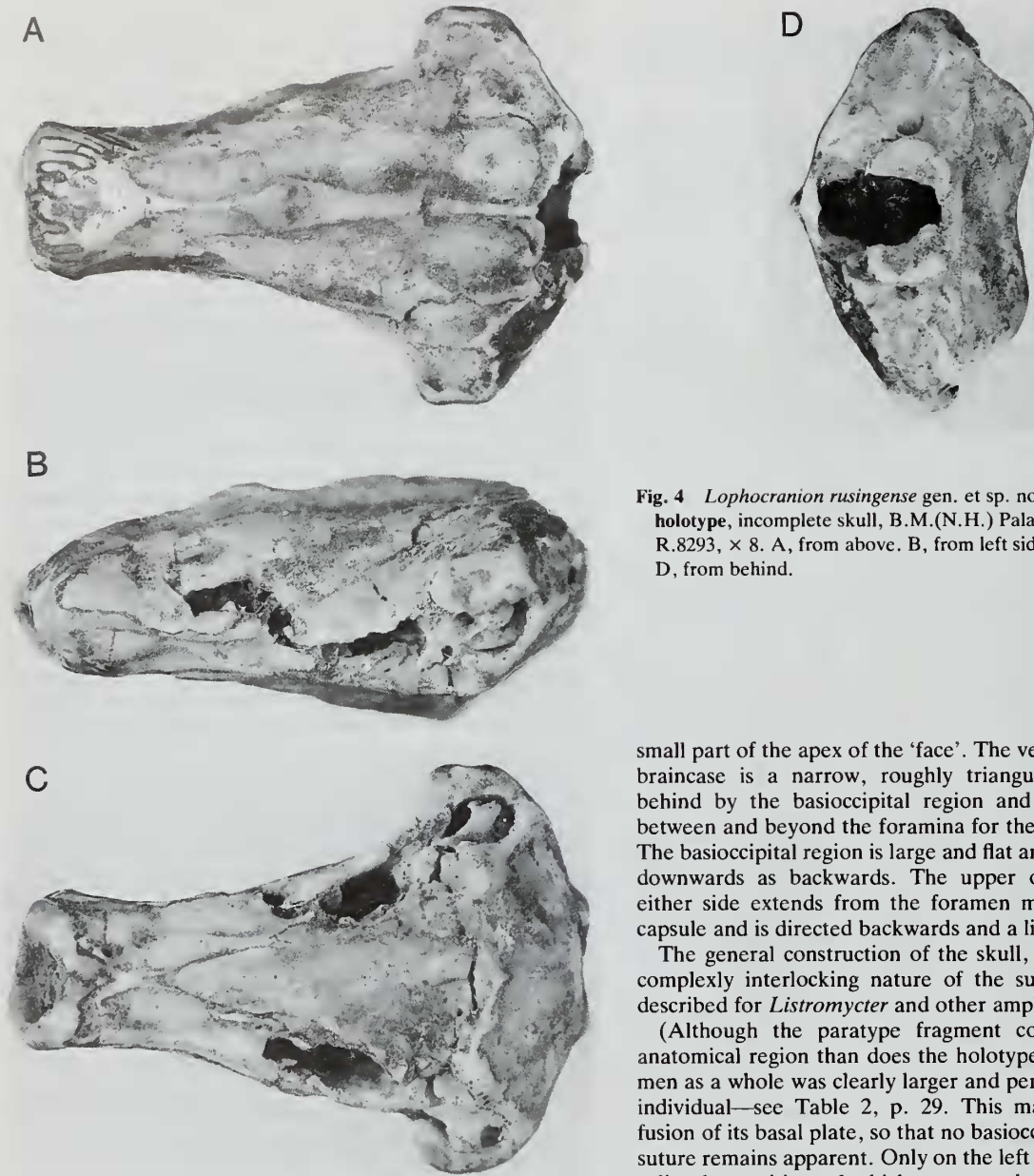
A

D

B

Fig. 4 *Lophocranion rusingense* gen. et sp. nov. Photographs of **holotype**, incomplete skull, B.M.(N.H.) Palaeont. Dept. no. R.8293, × 8. A, from above. B, from left side. C, from below. D, from behind.

C

presumably served for the usual tendinous attachments; immediately posterior to this the crest is flattened and then rises again to reach its highest point just anterior to the notch for the supraoccipital. A distinct edge at the posterior margin of the cranial roof separates it from the occiput.

The skull as preserved has therefore seven major surfaces. On either side is the outer surface of the braincase; posteriorly these two surfaces may together be regarded as a cranial roof, extending out more or less horizontally from the sagittal crest and running onto the otic capsule. Farther forwards each descends laterally in a convex curve towards the foramen for the Gasserian ganglion (the paratype is broken here); and farther forwards still, where the braincase is very slender, it descends quite steeply towards its lower rim and might justifiably be regarded more as a lateral wall than as a roof. At the very anterior tip of the specimen as preserved is a

small part of the apex of the 'face'. The ventral surface of the braincase is a narrow, roughly triangular area, bounded behind by the basioccipital region and tapering forwards between and beyond the foramina for the Gasserian ganglia. The basioccipital region is large and flat and directed as much downwards as backwards. The upper occipital region on either side extends from the foramen magnum to the otic capsule and is directed backwards and a little outwards.

The general construction of the skull, its solidity and the complexly interlocking nature of the sutures are much as described for *Listromycter* and other amphisbaenians.

(Although the paratype fragment comprises a smaller anatomical region than does the holotype, the former specimen as a whole was clearly larger and perhaps from an older individual—see Table 2, p. 29. This may account for the fusion of its basal plate, so that no basioccipital-basisphenoid suture remains apparent. Only on the left side is there a small split, the position of which suggests that it represents the remnant of a former suture between two bones.)

Parabasisphenoid (pbs) and '*element X*'

The median parabasisphenoid forms the greater part of the floor of the braincase. It consists essentially of a narrow triangle with its apex directed forwards, between and beyond the foramina for the Gasserian ganglia; the apex, which makes an angle of about 30°, is rounded off, although it may have extended farther forwards as a sharp cultriform process, the rounding off being due to postmortem rolling. The base of the triangle is the suture of the parabasisphenoid with the basioccipital; this runs more or less transversely except that on either side it makes one short, sharp zigzag halfway along its length and, in consequence, the triangle looks rather like a stylized drawing of a Christmas tree standing on a very short, wide pedestal. The external, ventral surface of the triangle is
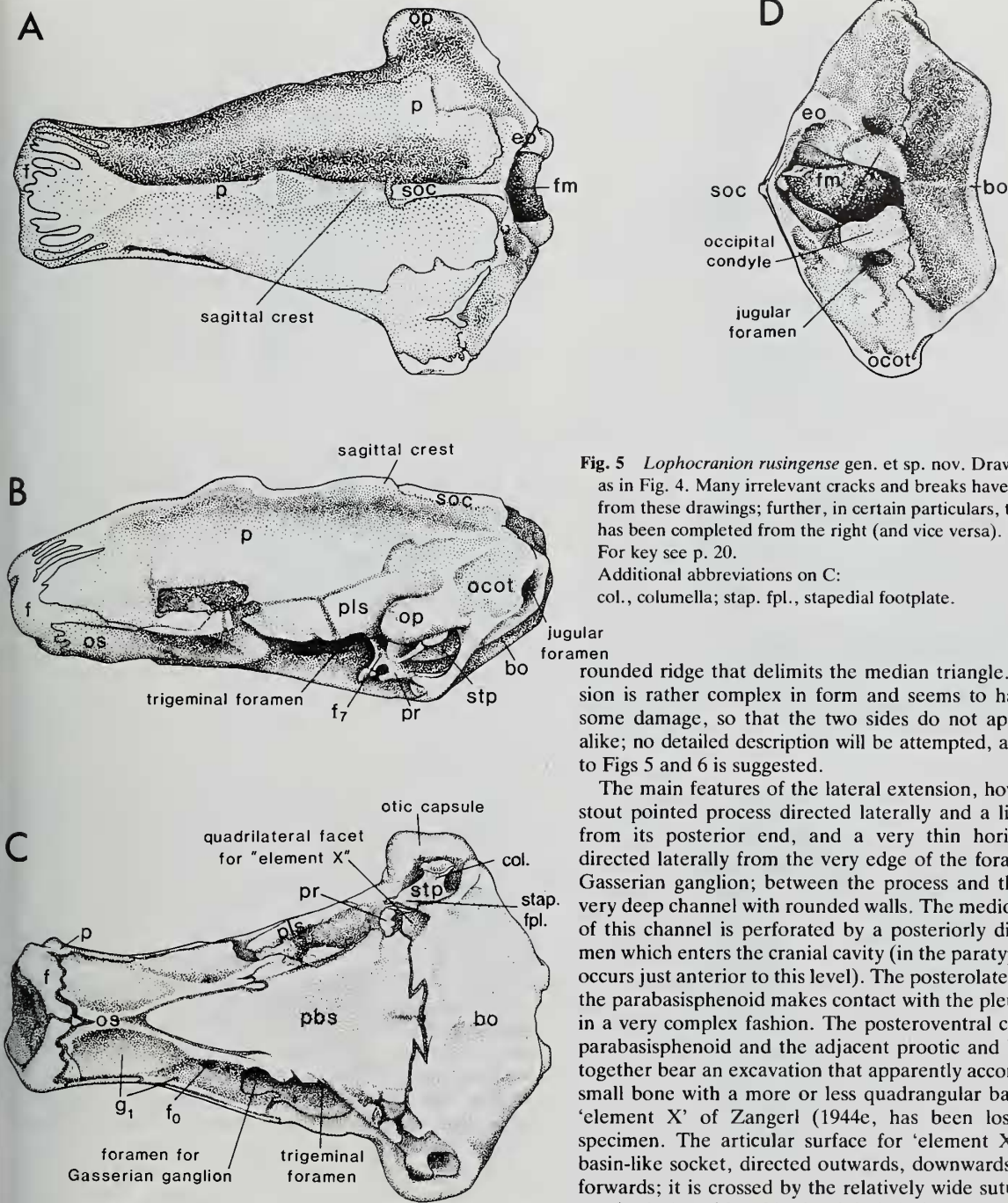
Fig. 5 *Lophocranion rusingense* gen. et sp. nov. Drawings, exactly as in Fig. 4. Many irrelevant cracks and breaks have been omitted from these drawings; further, in certain particulars, the left side has been completed from the right (and vice versa).
For key see p. 20.
Additional abbreviations on C:
col., columella; stap. fpl., stapedial footplate.

gently concave, the concavity being more transverse than anteroposterior.

The anterior third of the lateral margin of the parabasisphenoid sutures in a more or less straight line with the orbitosphenoid. At the level of the front end of the foramen for the Gasserian ganglion, however, the parabasisphenoid sends out a small lateral wing; at that point the suture between the parabasisphenoid and the orbitosphenoid becomes digitiform, terminating at the medial edge of the foramen a little way behind its anterior end. Posterior to this the parabasisphenoid forms the medial edge of the foramen; it extends dorsally and laterally on either side of the straight
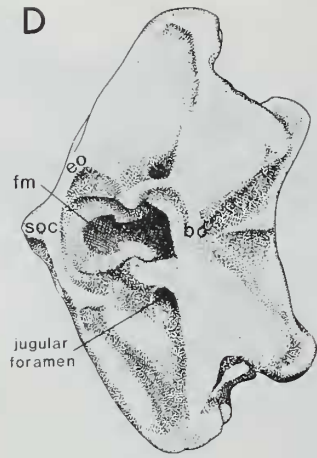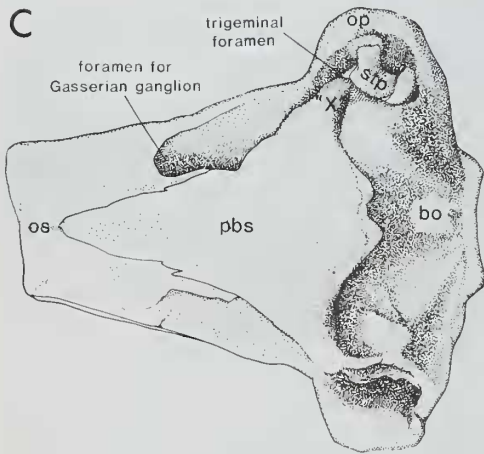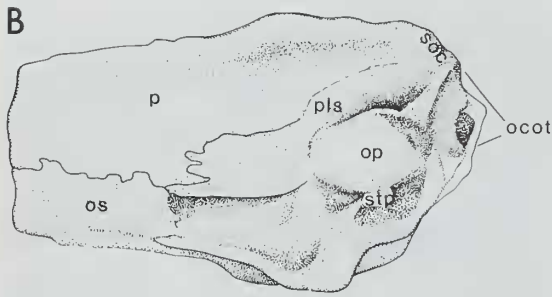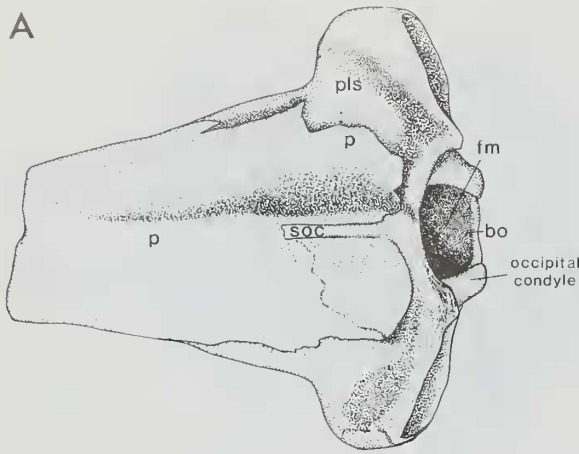
rounded ridge that delimits the median triangle. This extension is rather complex in form and seems to have suffered some damage, so that the two sides do not appear exactly alike; no detailed description will be attempted, and reference to Figs 5 and 6 is suggested.

The main features of the lateral extension, however, are a stout pointed process directed laterally and a little dorsally from its posterior end, and a very thin horizontal shelf directed laterally from the very edge of the foramen for the Gasserian ganglion; between the process and the shelf is a very deep channel with rounded walls. The medioventral wall of this channel is perforated by a posteriorly directed foramen which enters the cranial cavity (in the paratype the break occurs just anterior to this level). The posterolateral corner of the parabasisphenoid makes contact with the pleurosphenoid in a very complex fashion. The posteroventral corner of the parabasisphenoid and the adjacent prootic and basioccipital together bear an excavation that apparently accommodated a small bone with a more or less quadrangular base; this, the 'element X' of Zangerl (1944e, has been lost from this specimen. The articular surface for 'element X' is a deep basin-like socket, directed outwards, downwards and a little forwards; it is crossed by the relatively wide suture between parabasisphenoid and basioccipital. (It is unclear whether the element has indeed been lost from the paratype, or whether it fused to the posterior corners of the basisphenoid and abraded with these. Certainly there is no sharply defined facet and no trace of the triradial fossa.) It is also crossed by a canal, the foramen of which opens immediately anteroventral to the footplate of the stapes; the upper surface of the lost 'element X' formed the floor of the canal. (None of these canals is visible in the paratype and the entire area is solid. If the differences between the specimens are due to ontogenetic changes, one would then suspect that the absence of canals reflects either that the canals have closed, or that the fossil is broken within the 'element X' so that the canals are not exposed.)

Orbitosphenoid (os)

The orbitosphenoid forms the ventral surface of the braincase
between the region of the cranio-facial flexure and the
anterior end of the foramen for the Gasserian ganglion. Its
median part is underlain—and therefore covered in ventral,
i.e. external view—by the parabasisphenoid triangle just
described. In the midline there is a low flat-topped ridge,
separating the orbitosphenoid into two halves (although there
is no trace of a median suture). Anteriorly the orbitosphenoid
is bounded by the frontals meeting each other in the floor of
the braincase; the suture is more or less transverse but rather
irregular. The lateral surface on either side is simple and
externally concave; its anterior third is with a backwardly

directed process of the frontal, the rest is with the parietal.
Posteriorly the orbitosphenoid extends a short way along
both lateral and medial edges of the foramen for the Gasserian
ganglion on either side; its posterior termination on the
lateral edge abuts against the anterior termination of the
pleurosphenoid. Although the elongated foramen for the
Gasserian ganglion ends a little anterior to this point, it
continues farther forwards as a broad, shallow groove (g_1)
in the ventral surface of the orbitosphenoid which curves
gently outwards and tapers forwards to end near the point
where frontal, parietal and orbitosphenoid meet. On
the inner edge of this groove, about a quarter of the
way from the foramen for the Gasserian ganglion to the
frontal-orbitosphenoid suture, a small foramen (f_0)—
presumably for the optic nerve—enters the bone; it is directed
posteromedially.

Frontal (f)

Only the extreme posterior ends of the frontals remain; these
together form a ring around the front end of the cranial
region of the skull. (The frontals are missing entirely in the
paratype.) They are separated from each other only by a
convoluted median suture above and below the cranial cavity.
Posteriorly they suture with the orbitosphenoid below, by a
more or less transverse but rather irregular suture, and
elsewhere with the parietal. The fronto-parietal suture is
rather complex. Beginning in the dorsal midline, just below
the apex of the 'face', it proceeds laterally by a series of four
or five narrow interdigitations of progressively increasing
length; the front ends of the interdigitations lie at about the
same transverse level as the starting point, but their back ends

lie progressively more posteriorly. The first two or three are on the 'face', the last and most lateral two interdigitations are on the side of the skull. The last interdigitation of the frontal, seen in lateral view, appears to be directed backwards and upwards. From its base another process of the frontal, about as long as the last interdigitation but directed backwards and downwards, runs down between the parietal above and the lateral margin of the orbitosphenoid below. The most anterior part of the parietal, between the last interdigitation of the frontal above and this posteroventral process below, is broken off on the right side of the holotype. This break reveals that the frontal is more extensive internally and is merely overlapped by the parietal in this region; the parietal lies in a deep trough of the frontal, the bottom of which bears shallow longitudinal grooves.

Parietal (p)
The greater part of the external surface of the roof and sides of the braincase is formed by the unpaired parietal, which forms also the extreme posterior apex of the 'face'. Except in the anterior region, however, the roof and sides of the braincase are also formed in part by the fused pleurosphenoid, occipital and otic bones, henceforth to be referred to here as the occipito-otic complex (ocot). The parietal overlaps this complex posteriorly, but in the holotype described here parts of the parietal have been broken off and the resulting 'suture lines' are rather misleading; the true extent of the parietal is indicated by a depression in the occipito-otic complex which is bounded by a distinct rim. The irregular surface of the depression and the broken edges of the parietal indicate very clearly the complex interdigitating nature of the suture.

Posteriorly the parietal has a deep, very distinct median slot running forwards for about a quarter of its length; this accommodates the supraoccipital process, which thus forms the median portion of the sagittal crest in this region. The parietal-supraoccipital suture passes backwards down the side of this bar, parallel to the midline and very close to it. Just before reaching the back of the skull it curves outwards to run more or less parallel to the posterior margin of the skull roof in the region lateral to the foramen magnum. More laterally still it curves forwards again, passes medial to the otic capsule, and then continues forwards and a little downwards along the side of the braincase as the parietal-pleurosphenoid suture (in the paratype the edges are variably broken in this region); this is only very slightly irregular except in that, at its extreme anterior end, a short 'finger' of parietal points backwards and downwards towards the middle of the trigeminal foramen (the break is near the posterior third in the paratype). Forward of this point the ventral edge of the parietal reaches the lower rim of the braincase and sutures with the orbitosphenoid.

Anteriorly the parietal sutures with the frontal (missing in the paratype); this too has been described above. The sagittal crest on the parietal has already been dealt with in the general description of the skull.

Occipito-otic complex (ocot)
The posterior part of the skull is represented in this specimen by a single co-ossification, lacking apparent sutures but presumably of compound origin. Comparisons with descriptions of the skulls of lizards (Jollie 1960) and particularly of amphisbaenians (Zangerl 1944, Kritzinger 1946, Bellairs & Kamal 1980, Rieppel 1981) suggest that the complex includes the pleurosphenoid, supra- and exoccipital, pro- and opisthotic

bones; except for the supraoccipital all those bones are paired. They are here described in sequence without discussion of the position of the presumed lines of suture. While we thus follow other authors, we do so with some reservations since the true nature of the complex has yet to be studied—preferably on embryological material.

Pleurosphenoid (laterosphenoid) (pls)
The pleurosphenoid region of the occipito-otic complex (cf. Rieppel 1981) seems to form a considerable part of the roof and sides of the posterior region of the braincase; but, except for the posteroventral part of the lateral wall, immediately above the trigeminal foramen, it seems likely that it was generally overlain by the parietal. In the holotype the external exposures of the pleurosphenoid-supraoccipital appear to be rather greater than this because parts of the overlying parietal—at the back end of the skull, dorsomedial to the otic capsules—seem to have been lost. (Relatively more has been lost in the paratype, where the square lateral edges of the parietal confirm that these have been broken.) The anterior termination of the pleurosphenoid (missing in the paratype) is on the lateral edge of the trigeminal foramen, a short way behind the anterior end of the latter; here it abuts against the posterior termination of the orbitosphenoid. The pleurosphenoid is delimited above by the parietal, as already described; the suture is only very slightly irregular except in that, at its extreme anterior end, a short 'finger' of parietal points backwards and downwards towards the trigeminal foramen. Ventrally the pleurosphenoid forms the more or less straight lateral edge of the trigeminal foramen and then contacts the prootic, opisthotic and supraoccipital without apparent suture.

Supraoccipital (soc)
The unpaired supraoccipital adjoins the parietal anteriorly, the pleurosphenoids anteroventrally, the opisthotics laterally and the exoccipitals below. The only suture that can be discerned, however, is the suture with the parietal, described above. The external exposure of the supraoccipital consists essentially of four regions. Most distinct is the exposure of the supraoccipital process in the skull roof, which appears as a narrow, keeled, straight-sided bar fitting into the median slot in the parietal mentioned above; its anterior end, the processus ascendens, is not tapered but ends bluntly in a straight transverse line. There is a semicircular gap around its anterior end which was presumably filled with cartilage in the living animal (as in *Dalophia* and *Monopeltis*; Kritzinger 1946, Gans personal observation) and beyond this the ridge of the sagittal crest is continued forwards by the parietal as already described. The supraoccipital itself begins to widen backwards before the parietal sutures on either side begin to diverge, i.e. the parietal overlies it laterally towards the back of the skull.

Despite the lack of sutures, it may also be presumed that the supraoccipital forms:
1. A narrow strip along the posterior edge of the skull, the roof of which is not quite covered by the parietal.
2. That part of the skull roof that is posteromedial to the otic capsule.
3. The uppermost strip of the occipital surface of the skull.

Prootic (pr)
The element that we consider to be the prootic lies behind the trigeminal foramen, of which it forms the concave posterior

border; it contacts the parabasisphenoid medially and the pleurosphenoid (without suture) laterally. Posterolaterally it contacts the otic capsule, of which it may also form a part. From this region a short, stout process descends to the socket for the articulation of the 'element X' of Zangerl (1944; see below), of which it forms the anterolateral portion (and to which it is fused in the paratype). The anteromedial portion of 'element X' is formed by the parabasisphenoid and the posterior portion by the basioccipital (all of which are fused in the paratype). The suture with the basioccipital is presumed to be represented by the canal that runs across the articulation—as described in the section on the parabasisphenoid, p. 31—although the two elements seem to be continuous at the base of the canal (fused in the paratype). Posterolaterally this element is overlain by the anterior part of the stapedial footplate. Just anterior to its contact with the stapes two small foramina, one above the other, penetrate the bone; on the left side (f_7) they are very closely adjacent, on the right they are much farther apart. (A single large oval foramen lies in an equivalent position on each side of the paratype. It is uncertain whether a second foramen is covered by the stapes, yet these do not seem to be displaced.) These, from their spatial relations to the stapes, are presumed to be the facial foramina for the VIIth nerve.

As all the elements in this region are fused together, we must give our reasons for believing this particular part to be the prootic:
1. The element forms the posterior wall of the trigeminal foramen (Romer 1956: 28).
2. It is perforated by the two small foramina that carry the VIIth nerve; these lie just anterior to the extent of the stapes.
3. It forms the anterior part of the rim of the fenestra ovalis and supports the wide anterior flange of the stapedial footplate.
4. It lies immediately anteroventral to the otic capsule.
5. It lies lateral to the lateral termination of the basisphenoid-basioccipital suture (obliterated in the paratype).

Opisthotic (op)
The opisthotic forms the greater part of the otic capsule; it is a large, solid, rounded swelling that projects laterally from the posterolateral corner of the skull roof and overlies the fenestra ovalis. No sutures are visible, either on it or around it, but it is possible that the capsule includes also a contribution from the prootic. The rounded anterior face of this process apparently formed the articular surface for the cup-shaped head of the quadrate, a bone that is missing in all these specimens. The texture of the head is rougher than that of the cranial roof; in particular, the dorsolateral half is penetrated by numerous small pits as well as by one fairly large foramen (not apparent on either side of the paratype) placed along the dorsal edge of what is here interpreted as being the articular surface.

Exoccipital (eo)
Most of the upper part of the occipital surface of the skull, facing upwards and backwards on either side of the foramen magnum, is presumably formed by the exoccipitals. As mentioned above, the uppermost strip of this surface is probably formed by the supraoccipital, but no suture can be seen. On each side a slightly irregular suture (fused in the paratype) runs from beneath the otic capsule and passes below the exoccipital to reach the bottom of the foramen magnum; beneath this is the basioccipital. The large oval occipital

condyle, the back of which is strongly abraded (mostly missing in the paratype) is thus formed jointly by the basioccipital and the exoccipitals. On either side of the occipital condyle, within the exoccipital, is the jugular foramen (for the IXth, Xth, XIth and XIIth cranial nerves); while it appears as a single opening, it is actually a somewhat convoluted cup-shaped depression containing one lateral, two ventral and at least two anterior foramina penetrating deeply (these are not clear in the paratype). The exoccipital is in contact with the otic capsule, more specifically (one presumes) with the opisthotic, but again the suture is obliterated.

Basioccipital (bo)
This element forms essentially the lower part of the occipital surface (partially broken out in the paratype), a large flat area directed as much downwards as backwards. Its upper suture with the exoccipitals and its lower suture with the parabasisphenoid have already been dealt with in the respective descriptions of those bones. (All are fused in the paratype.) As also mentioned above, it contributes towards the formation of the occipital condyle. Laterally it contacts the otic capsule above and the fenestra ovalis below; indeed, it forms the posterior and ventral margins of that aperture. More ventrally still, between the fenestra ovalis and the parabasisphenoid, it contacts the prootic; together with the latter two elements it forms the socket-like articulation for the 'element X' of Zangerl (1944).

Stapes (stp)
The large fenestra ovalis is closed by the more or less oval footplate of the stapes, which seems to extend forwards beyond the margins of the fenestra. From this, directed not only outwards but also a little upwards and backwards, projects the short, laminar columella (missing on the right side of the paratype). The columella is supported by a buttress running anteroventrally.

Phylogenetic position
The phylogenetic position of *Lophocranion* is especially difficult to determine; the remains of the animal consist of little more than the braincase, which is very constant in structure throughout the Amphisbaenia. It is easier to determine what *Lophocranion* is not than what it is.

Rusinga, where the *Lophocranion* material was found, is not far outside the somewhat restricted geographical range of the Recent Trogonophidae (north-west Africa; the 'horn of Africa' and Socotra; and southern Arabia and the lands around the Persian Gulf). But the Trogonophidae may at once be excluded from consideration. *Lophocranion* has a triradiate boss on the sagittal crest which may have served for the attachment of tendons from the axial musculature; none of the trogonophids possesses that character, although it is found in several other amphisbaenians (Amphisbaenidae *sensu* Gans 1967a). The form of the processus ascendens of the supraoccipital is also characteristically amphisbaenid in *Lophocranion*; in the trogonophids its structure is typified by that of *Trogonophis* itself, of which Gans wrote (1960: 151) 'The processus ascendens must not be considered to be an actual process here. Because the cranial plates overlap widely rather than join by suture, the processus is actually that portion of the supraoccipital exposed between the two posterior lobes of the parietal. There is no cartilaginous plug or foramen apparent at the very tip of the processus.'

Lophocranion is therefore likely to be an amphisbaenid. But it cannot be placed among the horizontally flattened,

shovel-snouted forms (a) because the anterior part of the cranial region is not shortened (it is relatively much longer even than in *Listromycter*, where the shortening is less marked than in Recent shovel-snouts), and (b) because the cranio-facial angle is only about 20°. Nor can it be placed with or near any genera with vertically compressed skulls, such as *Ancylocranium* or *Geocalamus*; in those genera the braincase is definitely oval in section, higher than wide. It is therefore probable, more specifically, that the new form is one of the more generalized, round-headed amphisbaenids.

The Recent amphisbaenids of Africa include four such genera: *Chirindia*, *Cynisca*, *Loveridgea* and *Zygaspis*. All are much smaller than *Lophocranion* (and also smaller than most of the species from South America: see Gans 1968, 1974). Indeed, none of those four African genera has a skull longer than 13 mm, whereas the total length of the skull of the *Lophocranion* holotype is estimated to have been about 17 mm (and that individual is considered to have been a juvenile, the paratype being much larger still). The braincase of *Lophocranion* appears to be altogether more slender and elongated, the distance between the fenestra ovalis and the fronto-parietal suture being greater than the distance between the fenestra ovalis and the occiput. None of the four African genera mentioned above has a processus ascendens that projects relatively as far forwards into the back of the parietal, none has a sagittal crest, and none has a braincase of the same outline (in particular, the otic capsules of *Lophocranion* seem to project more laterally, those of the Recent forms more anterolaterally). In addition, *Loveridgea* differs from *Lophocranion* in that its fronto-parietal suture is not nearly as digitiform as that of the Miocene genus, whilst that of *Chirindia* is almost straight.

On the other hand, in every one of the features mentioned above *Lophocranion* is much more like the larger South American amphisbaenids or the Cuban *Cadea*. In particular, there is little to distinguish *Lophocranion* from the South American genus *Amphisbaena*, especially from the larger species (e.g. *A. alba*) of that complex and possibly polygeneric assemblage. Resemblances lie in the pronounced sagittal crest, the widening of that crest just anterior to the supraoccipital tip, the transverse crest of the supraoccipital, and the marked lateral expansion of the temporal lobes on so slender a braincase. Indeed, we cannot yet establish any characteristics in which the preserved portions of the braincases of *Lophocranion* differ from those of *Amphisbaena*.

It must be pointed out that little is known of the variability within the genus *Amphisbaena*. Such characters as the proportions quoted above and the development of a sagittal crest may well be dependent upon absolute size or stage of ontogeny. It is also possible that the characters in question may eventually turn out to be those of large, generalized amphisbaenians, rather than autapomorphies of a derived group.

The zoogeographical importance of *Lophocranion* may not be as great as would superficially appear. It is faintly possible that we might be dealing with a 'South American' form in Africa, but much more likely that (a) the characteristics of the posterior portion of the skull are much less diagnostic at the amphisbaenian species level than are those of the anterior portion, and (b) the aspects shown here represent an earlier grade of specialization still demonstrated in the fossil and retained in South American species but lost in the present-day African forms. Similarly, some early North American rhineurids show an amphisbaenid pattern (Estes 1975). In any case, it must be remembered that the comparison is between a Miocene member of an African lineage and extant members of the South American group. In this case we had three options:

1. To leave the Rusinga form unnamed, merely describing it as 'amphisbaenid gen. et sp. indet.' This has the disadvantage of complicating citation.
2. To assign the Rusinga form to the genus *Amphisbaena*, hitherto restricted to South America. This course of action might lead to the basing of important zoogeographical conclusions upon nothing more than the posterior parts of braincases, lacking all those elements that are generally used in diagnosing amphisbaenians.
3. To give a new generic name to the Rusinga form, even though it may later prove that the species is congeneric with certain South American species of *Amphisbaena* (or with Miocene populations ancestral to them or to modern African genera).

We have chosen the third option as being the least of three evils.

On the information now at our disposal we cannot go further than this. Additional studies, and perhaps the acquisition of new material, may lead to taxonomic conclusions that are less vague; and those, in turn, may prove to have interesting zoogeographical implications.

REFERENCES

Bellairs, A. d'A. & Gans, C. 1983. The reinterpretation of the amphisbaenian orbitosphenoid. *Nature, Lond.* **302** (5905): 243–244.
—— & Kamal, A. M. 1980. The chondrocranium and the development of the skull in Recent reptiles. *In* Gans, C. & Parsons, T. S. (eds), *Biology of the Reptilia* **11** (1): 1–263. London.
Berman, D. 1973. *Spathorhynchus fossorium*, a Middle Eocene amphisbaenian (Reptilia) from Wyoming. *Copeia*, New York, **1973** (4): 704–721.
Broadley, D. G. & Gans, C. 1969. A new species of *Zygaspis* (Amphisbaenia: Reptilia) from Zambia and Angola. *Arnoldia (Rhodesia)*, Bulawayo, **4** (25): 1–4.
—— —— 1975. Additional records for *Zygaspis niger* and *Z. quadrifrons*. *Herpet. Rev.*, Cincinnati, Ohio, **6** (1): 21.
—— —— 1978a. Southern forms of *Chirindia* (Amphisbaenia, Reptilia). *Ann. Carneg. Mus.*, Pittsburgh, **47** (3): 29–51.
—— —— 1978b. Distribution, variation, and systematic status of *Zygaspis violacea* (Peters) (Amphisbaenia Reptilia), endemic to southeastern Africa. *Ann. Carneg. Mus.*, Pittsburgh, **47** (14): 319–334.
——, —— & Visser, J. 1976. Studies on amphisbaenians (Amphisbaenia, Reptilia). 6. The genera *Monopeltis* and *Dalophia* in southern Africa. *Bull. Am. Mus. nat. Hist.*, New York, **157** (5): 311–486.
Estes, R. 1975. Lower vertebrates from the Fort Union Formation, Late

Paleocene, Big Horn Basin, Wyoming. *Herpetologica*, Chicago, **31** (4): 365–385.

—— 1983. Sauria terrestria, Amphisbaenia. *In* Wellnhofer, P. (ed.), *Handbuch der Paläoherpetologie* 10A. xxii + 249 pp. Stuttgart & New York.

Gans, C. 1957. 'Anguimorph' tooth replacement in *Amphisbaena alba* Linnaeus, 1758 (Reptilia: Amphisbaenidae). *Breviora*, Cambridge, Mass., **70**: 1–12.

—— 1960. Studies on amphisbaenids (Amphisbaenia: Reptilia), 1. A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. *Bull. Am. Mus. nat. Hist.*, New York, **119** (3): 129–204.

—— 1967a. A check list of Recent amphisbaenians (Amphisbaenia, Reptilia). *Bull. Am. Mus. nat. Hist.*, New York, **135** (2): 61–106.

—— 1967b. *Rhineura*. *In* Dowling, H. G. & McCoy, C. J. (eds), *Catalogue of American amphibians and reptiles*: 42.1–42.2. Gainesville, Am. Soc. Ichthyol. Herpet.

—— 1968. Relative success of divergent pathways in amphisbaenian specialization. *Am. Nat.*, Chicago, Ill., **102** (926): 345–362.

—— 1969. Amphisbaenians—reptiles specialized for a burrowing existence. *Endeavour*, London, **28** (105): 146–151.

—— 1971a. Studies on amphisbaenians (Amphisbaenia, Reptilia), 4. A review of the amphisbaenid genus *Leposternon*. *Bull. Am. Mus. nat. Hist.*, New York, **144** (6): 379–464.

—— 1971b. Redescription of three monotypic genera of amphisbaenians from South America: *Aulura* Barbour, *Bronia* Gray and *Mesobaena* Mertens. *Am. Mus. Novit.*, New York, **2475**: 1–32.

—— 1974. *Biomechanics: approach to vertebrate biology*. x + 261 pp. Philadelphia. [Reissued 1980, Ann Arbor.]

—— 1976. Three new spade-snouted amphisbaenians from Angola (Amphisbaenia, Reptilia). *Am. Mus. Novit.*, New York, **2590**: 1–11.

—— 1978. The characteristics and affinities of the Amphisbaenia. *Trans. zool. Soc. Lond.* **34**: 347–416.

—— 1987. Studies on amphisbaenians (Reptilia), 7. The small round-headed species (genus *Cynisca*) from western Africa. *Am. Mus. Novit.*, New York, **2896**: 1–84.

—— & Alexander, A. A. 1962. Studies on amphisbaenids (Amphisbaenia, Reptilia), 2. On the amphisbaenids of the Antilles. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **128** (3): 65–158.

—— & Broadley, D. G. 1974. A new dwarfed species of *Monopeltis* from the Middle Zambesi Valley (Reptilia: Amphisbaenia). *Arnoldia* (*Rhodesia*), Bulawayo, **6** (35): 1–5.

—— & Kochva, E. 1965 (1966). A systematic review of *Ancylocranium* Parker (Amphisbaenia, Reptilia). Notes on amphisbaenids 22. *Israel J. Zool.*, Jerusalem, **14**: 87–121.

—— & Kraklau, D. 1989. Studies on amphisbaenians (Reptilia), 8. Two genera of small species from East Africa (*Geocalamus* and *Loveridgea*). *Am. Mus. Novit.*, New York, **2944**: 1–28, 20 figs.

—— & Latifi, M. 1971. Redescription and geographical variation of *Monopeltis guentheri* Boulenger (Amphisbaenia, Reptilia). *Am. Mus. Novit.*, New York, **2464**: 1–21. [Reprinted 1972, *Archs Inst. Razi*, Tehran, **24**: 63–82.]

—— & Lehman, G. C. 1973. Studies on amphisbaenians (Amphisbaenia: Reptilia), 5. The species of *Monopeltis* from north of the river Zaire. *Occ. Pap. Mus. Zool. Univ. Mich.*, Ann Arbor, **669**: 1–34.

—— & Rhodes, C. 1967. *Chirindia* from Tanganyika (Amphisbaenia, Reptilia) [Notes on amphisbaenids no. 19]. *Ann. Carneg. Mus.*, Pittsburgh, **39** (1): 1–32.

Gilmore, C. W. 1943. Fossil lizards of Mongolia. *Bull. Am. Mus. nat. Hist.*, New York, **81** (4): 361–384.

—— & Jepsen, G. L. 1945. A new Eocene lizard from Wyoming. *J. Paleont.*, Tulsa, Okla., **19** (1): 30–34.

Hoffstetter, R. 1955. Squamates de type moderne. *In* Piveteau, J. (ed.), *Traité de paléontologie* **5**: 606–662. Paris.

Jollie, M. T. 1960. The head skeleton of the lizard. *Acta zool., Stockh.*, **41** (1–2): 1–64.

Kritzinger, C. C. 1946. The cranial anatomy and kinesis of the South African amphisbaenid *Monopeltis capensis* Smith. *S. Afr. J. Sci.*, Cape Town, **42**: 175–204.

Peters, W. C. H. 1882. *Naturwissenschaftliche Reise nach Mossambique auf Befehl Seiner Majestät des Königs Friedrich Wilhelm IV in den Jahren 1842 bis 1848 ausgeführt. Zoologie III, Amphibien.* xv + 196 pp. Berlin.

Rieppel, O. 1981. The skull and the jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. *J. Zool., Lond.*, **195**: 493–528.

Romer, A. S. 1956. *Osteology of the reptiles.* xxi + 772 pp. Chicago.

Vanzolini, P. E. [1951a]. *Evolution, adaptation and distribution of the amphisbaenid lizards (Sauria: Amphisbaenidae).* 148 pp. Thesis, Harvard Univ., Cambridge, Mass. (unpublished).

—— 1951b. A systematic arrangement of the family Amphisbaenidae (Sauria). *Herpetologica*, Chicago, **7** (3): 113–123.

Young, C.-C. 1961. On two new fossil lizards of China. *Vertebr. palasiat.*, Peking, **5** (2): 118–121.

Zangerl, R. 1944. Contributions to the osteology of the skull of the Amphisbaenidae. *Am. Midl. Nat.*, Notre Dame, Ind., **31** (2): 417–454.